

Chapter 5

Genetics of Port-Orford-Cedar

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Introduction

Importance of Genetic Resources

In order to promote and sustain health, biodiversity, and productivity of public forest resources, it is necessary to conserve the basic natural resources (water, soil, air, elements, and biota) and their functional processes. The genetic materials of the biota are fundamentally important natural resources, because genetic diversity among and within species is the basis for all biological diversity. Genetic diversity is essential for the survival and adaptation of species to new, changing environments. In addition, genes program the structure, function, and response of individual organisms to their environment. Together with other factors they determine the health and vigor of forest stands.

Genetic materials are subjected to natural processes that need to be understood and managed. The hereditary process, involving DNA self-replication and transmission of exactly one-half of the genes from each parent to their offspring, provides continuity and preservation of genetic material across generations and from cell to cell within the same individual. Because of heredity, offspring tend to resemble their parents. Therefore, by controlling the seed parents, managers can influence traits of the seedlot. In addition to this stable hereditary process, there is an evolutionary process involving selection, gene flow, mutation, and drift that cause changes in gene frequencies of populations. Management activities may simulate evolutionary forces, e.g. transplanting is a gene flow activity and selection of seed parents is a selection activity.

Genetic Structure of a Species



These evolutionary forces, plus the mating pattern of the species, results in a unique pattern of genetic variation for each species. Knowledge of the diversity and distribution of genes among and within populations of a species is crucial to genetic management, whether the purpose is to develop strategies to conserve natural populations or to improve breeding populations. A genetic inventory that describes the extent and pattern of genetic variation across the range of a species is one prerequisite to protecting the adaptive structure of a species and to monitoring genetic changes due to pests, climate extremes, and management practices.

Figure 5.1—Port-Orford-cedar branch bearing cones

In the major conifers, the genetic composition of natural populations usually changes along environmental gradients (clinal variation pattern). Typically, forest trees adapt to temperature and moisture gradients which, in turn, are often associated with geographic variables such as elevation, latitude, or distance from the ocean. Trees may evolve adaptations to rather abrupt and major changes in soil parent material over short distances (edaphic ecotypic variation pattern). As a rule, trees become generally, but not perfectly, adapted to local environments. This is because trees often require decades to reproduce, the environment is constantly changing, and other forces (e.g. gene flow, recombination, and genetic drift) may counteract the effects of selection. The genetic gradients commonly follow paths from milder and more productive sites to harsher and less productive environments. Parent trees from the mild, productive sites usually produce offspring that are faster growing, grow for a longer period of time during the year, and in some situations may be less resistant to drought and cold stress than those from harsher environments.

Measurement of Genetic Structure: genetic tests

Genetic differentiation patterns in adaptive traits along geographic, elevational, and edaphic gradients must be known before seed can be successfully transferred during reforestation. The genetic architecture of commercial conifers in California and Oregon has been well-studied using provenance field trials (common garden studies) and electrophoretic analysis of certain enzymes (allozyme studies), the key tools for measuring and understanding natural genetic variation patterns. DNA technologies are now used to complement these two common methods.

Allozyme studies produce relatively quick and inexpensive results. Allozyme techniques provide useful quantitative measures of genetic structure (pattern of variation among and within populations), genetic diversity (heterozygosity), and mating system (outcross percent) for certain enzymes. These enzymes are common to a wide variety of species, and since they exhibit Mendelian genetics, they are called allozymes. The allozyme parameters allow standards for comparisons across species and can provide quantitative information about genetic systems that characterize different species. Some practical limitations in allozyme studies are the small portion of the genome expressed, the gene level of measurement, the neutrality of many allozyme genes, and the general absence of measurement of adaptive traits. Allozyme studies are not a replacement for common garden trials, because allozymes can not show adaptive responses of trees to field environments and allozymes tend to underestimate variation among populations, especially in conifers. However, multi-locus allozyme variation may indicate underlying adaptive variation and therefore may be useful for delineating tentative breeding zones when the multi-locus pattern is closely correlated to geographic or environmental variables (Westfall and Conkle 1992).

Seed zoning must be primarily based on common garden field studies where whole plant response can be evaluated. Common garden studies with multiple and contrasting test environments provide direct comparisons of genetic materials for many adaptive traits tested under field conditions. With seed sources tested over multiple sites, the pattern of adaptive response can be determined for each seed source and then related to presumed natural selective factors at point of origin. For example, if natural selection were a primary force, the pattern of differences among populations for adaptive traits should correspond with a pattern of environmental differences where populations originated. Allozyme and common garden studies conducted together complement one another, providing both basic genetic parameters and practical field expression of adaptive traits.

Genetic Variability

During the previous two decades, several genecological studies have been conducted on Port-Orford-cedar. Allozyme studies and common garden studies are two key tools used for measuring and understanding natural genetic variation patterns.

Allozyme Studies

In 1991, investigators examined the allozyme variation of nine Port-Orford-cedar stands in California that represented the extremes in elevation, latitude, and longitude of the species range in that state (Millar and Marshall 1991). Seven of the stands were located in the coastal range, while two came from interior, disjunct populations. Port-Orford-cedar was found to be moderately variable in allozymes (less than widespread, dominant species such as Douglas-fir). The inland populations differed in allele frequencies from coastal populations, being more monomorphic, had higher frequency of common alleles, and had a lower percent of polymorphic loci. In addition, the inland populations were, on the average, only one-half as variable as the most variable coastal population. Not only was there a clear separation between coastal and inland groups, but also the two inland populations were distinct from each other. On the average, for all stands studied, 5 percent of the total allozyme variation was attributed to differences among stands and 95 percent to differences within stands. Much greater differences occurred among stands in the inland than in the coastal group, suggesting that inland populations may have been isolated from each other long enough for genetic drift or selection effects to cause differentiation. As a group, the inland populations within the Sacramento and Trinity River drainages (Trinity and Scott Mountains) had greater genetic diversity among stands and less within stands. Within the coastal group, the Horse Mountain population had enough unique alleles and divergent frequencies to be relatively distinct from other coastal populations. The Shelly Creek population displayed high genetic diversity within its stands.

Millar et al. (1991) examined the relationship between allozyme diversity and ecological diversity (soil and elevation). To determine if there was a correlation within a local area, foliage was sampled from trees along the Middle Fork and South Fork of the Smith River, at low and high elevations, and on fertile and ultramafic soils. These contrasts have been found by ecologists to significantly discriminate between Port-Orford-cedar plant associations in northwestern California. Ecological data for stands between plant associations were strongly differentiated by elevation and soil fertility, and Millar et al's (1991) results showed strong correlations of allozyme diversity with ecological habitat over short distances.

Elevation was a stronger factor than soil type in determining genetic differentiation (48 percent of the genotypes were different between elevations). The effect of soil type varied depending on elevation. At low elevations, differences between soil types were nearly as great as the overall elevation effect, but at high elevation the soil effect was relatively low. At low elevations, the mismatch of genotypes between soil types was 49 percent, while at high elevation the mismatch was only 14 percent. Thus, habitat conditions at high elevations were apparently severe enough for selection to mask or override the effect of soil type. Soil fertility more strongly separated plant associations than genetic data.

There was a trend in both plant associations and genetic data (weaker in genetic data) for higher diversity at low elevations. This study suggested that seed collected from coastal California should be identified by elevational zones and, at the low elevations, by ultramafic and non-ultramafic soils.

In 1992, investigators once again examined allozyme variation of Port-Orford-cedar stands, but on a much wider scale (Millar, et al. 1992). The sources came from 46 stands in California and 36 stands in Oregon. Additional single-tree collections were made to fill gaps between stands and to sample unusual sites. The mean allozyme diversity was slightly higher for Oregon than for California stands, but with the range of diversity among stands in California being greater. Low within-stand diversity was found scattered across the range in Oregon, but only occurred within the California groups of stands in the Sacramento and Trinity drainages. In each state, the pattern of allozyme variation among populations was strongly linked with latitude, longitude, and elevation. In Oregon, the cline was strongest along north-south (latitude), weaker along east-west (longitude), and weakest along elevational gradients. In California, the cline was strongest along east-west (longitude) with elevation being a relatively strong determinant of allozyme diversity.

Common Garden Studies

Despite their considerable utility, allozyme studies cannot show adaptive responses of trees to field environments. Thus, in 1995, a major effort began to establish range-wide common garden tests to further evaluate the genetic variability within Port-Orford-cedar.

Seed was collected from 344 healthy parent trees on federal land from 1991 through 1994 by the Forest Service and Bureau of Land Management (BLM). Stands were sampled throughout much of the species' range from the extreme northwestern portion (Oregon Dunes) to the extreme southeastern stands (Pond Lily Creek, Upper Trinity River). Sample trees were grouped into 10 regional watersheds, six in Oregon and four in California, and into 52 stands, 36 in Oregon and 16 in California. However, the distribution of watersheds, stands within watersheds, and trees within stands, was not even. Two different hierarchical models were employed to partition the genetic effects: 1) ecological or watershed model with watersheds, stands, and families, and 2) a breeding model with breeding zones, seed zones, and families (tables 5.1 and 5.2). The grouping of trees into four tentative breeding zones was based on combinations of similar seed zones with boundaries as currently drawn (USDA 1969 and 1973). These tentative breeding zones were compared to the ecological (watershed) model. In 1996, a short-term and a long-term common garden study were established. The short-term study was planted in raised beds at two nurseries using 298 of the families. Four sites in 1996 and one site in 1998 were out-planted for the long-term study using 266 of the families. In addition, the 344 families were tested for disease resistance (refer to Chapter 6)⁹.

Short-term raised bed study design—In spring 1996, 1-0 seedlings grown in Korbels, California, were transplanted to two locations, Dorena Tree Improvement Center, Cottage Grove, Oregon, and Humboldt Nursery, McKinleyville, California (figs. 5.2 and 5.3). The Humboldt site is 1.9 miles from the ocean at 249 feet elevation.

The experimental design was a randomized, complete block with six blocks and 298 families. At Dorena, all blocks were located in raised beds with organic rooting medium, but three blocks were shaded with 47 percent shade-cloth during the growing season (fig. 5.3). At Humboldt, three blocks were in conventional nursery beds with mineral soil, while three blocks were in raised beds with organic rooting medium and partially shaded by adjacent trees. The spacing of seedlings was slightly greater at Dorena's raised beds compared to Humboldt's conventional beds and raised beds.

⁹ Through international cooperation in genetic conservation of forest trees, these seed sources and the study design were also replicated in several out-plantings in Spain.

Table 5.1—Port-Orford-cedar population samples by watershed for the common garden study (ecological model)

Regional Watershed	No. Stands	No. Trees	Elevation Range	Latitude Range (deg)	Longitude Range (deg)
Trinity	2	9	5200 – 5299 feet	41.0885 - 0.1255	122.4720 - 0.5301
Sacramento	3	30	3750 – 5200 feet	41.2200 - 0.2500	122.3959 - 0.4600
Klamath	3	24	2999 – 4501 feet	41.0000 - 0.8234	123.4651 - 0.9000
Smith	8	40	1319 – 5200 feet	41.7237 - 0.9657	123.6493 - 124.0690
Illinois	2	13	3360 – 3501 feet	42.0332 - 0.1250	123.3553 - 0.5535
Applegate	4	29	2300 – 4501 feet	42.1188 - 0.2073	123.2789 - 0.4057
Rogue	6	28	2178 – 3599 feet	42.4277 - 0.6917	123.7248 - 124.2843
Coquille	18	82	400 – 2749 feet	42.7083 - 43.2600	123.7800 - 124.1333
Dunes	4	26	49 – 194 feet	43.3400 - 0.4500	124.2500 - 0.3400

Table 5.2—Port-Orford-cedar population samples by tentative breeding zones for the common garden study (breeding model)

Breeding Zones	Seed Zones	Watersheds	Families (no.)
North Coast	071, 072, 081	Dunes, Coquille, Sixes, Rogue	155
North Interior	511, 512	Applegate, Illinois, Smith	57
South Coast	091, 301, 302	Smith, Klamath	47
South Interior	331, 521	Trinity, Sacramento	39

**Figure 5.2—Raised bed, short-term common garden study at the Humboldt Nursery site, McKinleyville, California**



Figure 5.3—Raised bed, short-term common garden at the Dorena Tree Improvement Center, Cottage Grove, Oregon

Short-term raised bed study: Height growth results (Kitzmilller and Snieszko 2000)—The environmental components, transplanting location and “shade” treatments, had significant effects on 2-year height growth (Appendix D presents the analysis of variance [ANOVA] tables and means). Surprisingly, the inland location had superior height compared to the coastal location both years, and “shading” was inferior to open sun the second year. The height growth response of Port-Orford-cedar families from different geographic regions and stands revealed a strong genetic structure with a well-defined geographic pattern. Height potential was highly related to genetic source at the watershed, stand, and family levels. The genetic structure for early height is described in the proportion of total variance residing at various source levels. Genetic main effects were strong and accounted for 47.5 percent (watershed = 37.4 percent, stands within watershed = 3.4 percent, families within stands = 6.7 percent) of the total variability. Strong clinal patterns were found for height potential with source elevation, latitude, and longitude. Genetic by environment (G-x-E) is a parameter used to assess changes in the performance of genotypes when grown under different environments. G-x-E interaction accounted for 6.1 percent of the variability and blocks accounted for only 9.9 percent. G-x-E interactions, though statistically significant at watershed and family levels, were minor sources of variability in height, and were due to scale effects rather than rank changes. Southern and high elevation inland sources had low growth potential at both locations, while northern and low elevation coastal sources had high growth potential. Second year total height decreased 11.1 inches (28.2 centimeters) per 3281 feet (1000 meters) increase in source elevation. Trees from the low elevation Sixes/Elk watershed averaged 60 percent taller than those from the high elevation Trinity watershed. Trees from low elevation, northern, and coastal sites had less mortality, higher seed weight and higher filled seed percent.

These tentative results show population structure and geographic patterns similar to, though much stronger than, the allozyme studies previously mentioned. Current results suggest that gene conservation practices should encompass, 1) seed zoning by watershed, subdivided by elevation bands, and 2) protecting the broad gene base for growth, including the adaptive extremes near the northern and southern limits.

Short-term raised bed study: Variation in height growth phenology (Zobel et al., in press)—Timing of height growth was determined for 54 of the families in the short-term raised bed study. Measurements were made during the second year of growth. The proportion of early-season growth declined and the proportion of late-season growth increased with changes in seed source location from high to low elevations, from south to north, and from east to west. This pattern was parallel to that of seedling height and of actual elongation in each of three periods during the growing season. The tallest trees (from the Oregon coast near the species' northern range limit) grew more in each period, but had the greatest proportion of late-season height growth. Planting such genotypes where late summer drought or early frost is common may threaten their survival. Use of breeding zones that limit genotype transfer distance may avoid such damage. Seedlings grown at the coastal nursery had a lower proportion of early-season growth and more in late-season than seedlings grown inland.

Short-term raised bed study: Variation in water relations characteristics of leaders (Zobel et al. 2001)—Water relations attributes of immature tissues of the terminal leader and its branches were measured on a subset of the short-term raised bed study families. Leader tissue provided consistent data and allowed interpretations directly useful for assessing effects on height growth. Osmotic potentials were higher than reported for most conifers. Osmotic potentials declined at both nurseries as the season progressed. The osmotic amplitude (osmotic potential at full turgor - osmotic potential at zero turgor) also increased during the season. Osmotic potential at full turgor was more negative and osmotic amplitude greater at the inland nursery than at the coastal nursery. Correlations with geographic location of the seed sources were weak. The small size of significant differences among families, nurseries, and sampling periods, and some inconsistencies among attributes measured, suggest that many of the differences may be of marginal physiological significance. However, correlations with plant size and timing of height growth suggest that, as one progresses from high elevation, southeastern locations toward the northwestern coast, where seedlings become larger and grow more late into the season, the relative water content at zero turgor increases, osmotic potential at zero turgor declines, and the tissue elasticity index rises. Larger genotypes thus appear to be less desiccation tolerant. When selecting genotypes for planting outside their native habitat, decisions based on the clear geographic patterns in tree size and timing of growth, reported elsewhere, should effectively account for the differences in water relations that appeared in this study.

Long-term common garden out-planting study—Short duration tests in low-stress nursery environments are not well suited for the expression of cumulative response to environmental stresses. Long-term field common garden studies are designed to reveal adaptive-based G-x-E interactions for guiding seed zoning and transfer (figs. 5.4 and 5.5). Four common garden sites were planted in 1996: Humboldt Nursery in McKinleyville, California, Trinity Lake on the Shasta-Trinity National Forest, and Althouse and Chetco on the Siskiyou National Forest. In 1998, an additional site, Battle Axe, was established on the BLM Roseburg District, which expanded the original 266 families to include samples from the northeast part of the range of Port-Orford-cedar. Height measurements have been taken on the Humboldt and Trinity Lake sites. Results show that watershed mean three-year height was inversely related to survival at the inland Trinity Lake site. North coastal watersheds, although much taller, had 60 to 70 percent survival, while extreme southeastern interior lots had 90 percent survival. Overall plantation growth and survival were better at the coastal Humboldt Nursery field site. A geographic cline in height growth was associated with latitude, longitude, and elevation of seed origin.

Northern, low elevation, coastal seed sources grew taller than southern, high elevation, interior sources at both plantation sites. However, these faster growing sources also showed the greatest relative reduction in growth and survival when planted at the inland Trinity Lake site.



Figure 5.4—Long-term out-planting site at Weaverville-Trinity Lake, California



Figure 5.5—Long-term out-planting site at Humboldt Nursery, McKinleyville, California

Seed Zones and Breeding Zones

General adaptation of trees along major geographic gradients is the basis for seed zoning. Seed zoning is a management tool that is used to protect the natural genetic structure of adaptive traits in forest tree species against undesirable gene transfer from their natural origin to planting sites. California and Oregon conifers have adapted through natural selection to temperature and moisture gradients and to different soil parent materials. These gradients are often associated with elevation, latitude, and distance to the ocean. Seed zones based on these geographic variables afford protection against dysgenic seed transfers. The purpose of seed zones is to partition the region into adaptively-similar zones within which wild seed collections of native trees can be freely moved without problems of maladaptation.

Geographic seed zones may require further subdivision of seedlots based on adaptation to extreme soils types. Genetic diversity in a natural forest within a relatively small geographic area presents a challenge. Are these differences adaptive in nature or are they simply vital components of a diverse natural breeding population? Managers must decide what seed trees to select and whether to keep seed separate or mix seeds from mild and harsh sites together, and if so, in what proportions. Strategies may favor either mixing seed parents within zones or keeping seed separate by local site. For species such as Port-Orford-cedar that occur on both ultramafic and granitic soils, there may be sufficient adaptive genetic differentiation to warrant separate seed lots for these extreme soil types within a geographic seed zone. Because seed zones are a practical tool, they must be large enough to be economical and easy for people to use, yet small enough to protect natural patterns of adaptation for the species.

Breeding zones have a similar purpose as seed zones except that seeds from selective breeding orchards are deployed instead of wild seeds. Breeding zones may be broader than seed zones provided that selected genetic stock has been proven through field-testing to be broadly adapted.

The genetic variability studies completed so far for Port-Orford-cedar indicate geographic zoning based on major watersheds or seed zones in combination with elevation bands. Preliminary breeding zones have been delineated, and will be used to guide seed transfer and selective breeding activities. Elevational bands should be no greater than 1,640 foot (500 meter) intervals up to 3,281 feet (1000 meter) elevation, and then becoming 820 foot (250 meter) intervals between 3,281 and 6,562 feet (1,000 and 2,000 meter) elevation. In this breeding zone designation, seed zones and/or portions of watersheds adjacent to one another within the coast or interior have been combined within these elevational bands. Geographic seed zones or breeding zones may require further subdivision of seedlots based on adaptation to extreme soil types. Species, such as Port-Orford-cedar, that occur on both ultramafic and granitic soils, may have sufficient adaptive genetic differentiation to warrant separate seed lots for these extreme soil types within a geographic seed zone.

Port-Orford-Cedar Breeding Block Designations

A breeding block designates the geographic area that envelopes a number of breeding zones. Breeding blocks have been delineated on the basis of a genetic common-garden study (Kitzmilller and Snieszko 2000) and general knowledge of southwestern Oregon and northern California species genecology (fig. 5.6). The common-garden study noted genetic variation associated with latitude, longitude, and elevation of the seed sources. Additional studies (Millar et al, 1991; Zobel et al, in press) have also noted differences

between the coastal and inland sources of Port-Orford-cedar. These breeding blocks have been delineated on the basis of this perceived genetic structure. Breeding zones are represented by elevation bands within the respective breeding blocks, and designate units of land in which improved populations (via genetic testing and breeding activities) are being developed. The elevation bands are: 1) less than 1,500 feet, 2) 1,501 to 3,000 feet, 3) 3,001 to 4,000 feet, 4) 4,001 to 5,000 feet, 5) 5,001 to 5,500 feet, 6) 5,501 to 6,000 feet, and 7) 6,001 to 6,500 feet. An elevation band within a breeding block constitutes a single breeding zone. Table 5.3 summarizes the six blocks depicted on the map.

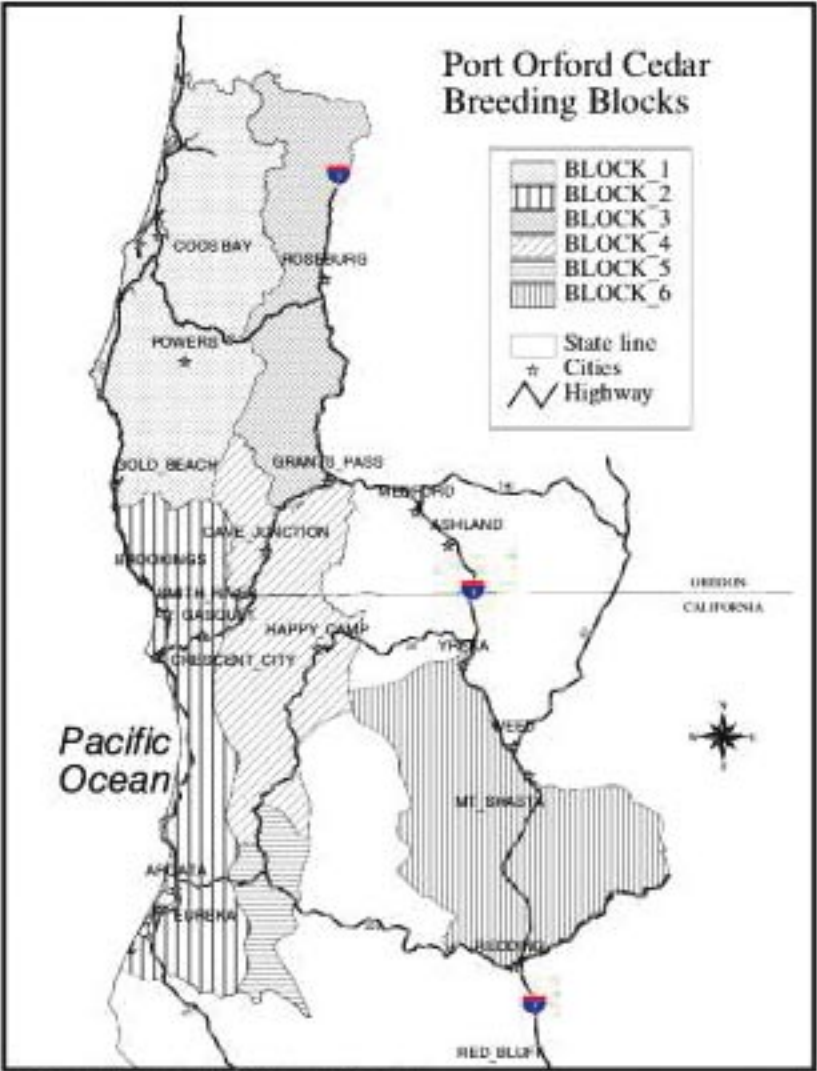


Figure 5.6—Port-Orford-cedar breeding blocks

Table 5.3—Description of location and seed zones for Port-Orford-cedar breeding blocks

Breeding Block	General Geographic Area	Reference to State Tree Zones (USDA 1969 and 1973)
BB1	North coast range of Port-Orford-cedar from Oregon Dunes to Gold Beach, Oregon	OR zones 071, 072, and portion of 081
BB2	South coast range of Port-Orford-cedar from Gold Beach, Oregon to Eureka, California	Portions of 082 and 090 (OR) and 091 and 092 (CA)
BB3	North inland range of Port-Orford-cedar from near Umpqua to near Provolt, Oregon	Portions of OR zones 270, 081, 511, and 512
BB4	South inland range of Port-Orford-cedar from Provolt, Oregon to near Orleans, California	Portions of 081, 082, 090, 511 (OR), 512 (OR and CA), and 301, 302 (CA)
BB5	Isolated Humboldt population(s) near Willow Creek, California	Portion of 303 (CA)
BB6	Range of Port-Orford-cedar in upper Trinity and Sacramento Rivers in California	Portions of 331 and 521 (CA)

Implications for Genetic Conservation

Management practices could be directed at protecting the range of genetic sources using both in situ and ex situ measures.

The adaptive genetic structure of Port-Orford-cedar is strongly differentiated at the regional watershed level and at the tree-to-tree level within a stand. A priority for conserving genetic populations could be to protect large stands in each major watershed. More stands could be sampled to represent low elevation, south coastal soil ecotypes and the interior higher elevation watersheds, where stands often are small and the range is fragmented. In small stands, favor those with 50 or more interbreeding trees.

Continued protection of Port-Orford-cedar in Research Natural Areas, Botanical Areas, and other existing forest reserves is warranted. New conservation units and conservation areas could be identified where current coverage has gaps. In California, there are apparent gaps in the northeastern and west-central portions of the coastal distributions and in the upper Trinity River drainage. In Oregon, large stands of Port-Orford-cedar in the Sixes and Elk River watersheds could be conserved for high growth potential, high root disease resistance, and high genetic diversity.

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